Interactions Among *Helicoverpa armigera* (Lepidoptera: Noctuidae), Its Larval Endoparasitoid *Microplitis croceipes* (Hymenoptera: Braconidae), and *Bacillus thuringiensis*

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ABSTRACT Interactions among *Helicoverpa armigera* (Hübner), its larval endoparasitoid *Microplitis croceipes* (Cresson), and *Bacillus thuringiensis* Berliner were evaluated under laboratory conditions. Prefeeding *H. armigera* with lethal concentrations (0.08 and 0.16 mg/g) of Dipel (*B. thuringiensis* subsp. *kurstaki* strain HD-1) did not prevent *M. croceipes* from ovipositing in the infected host larvae. Development of parasitoid immatures in host larvae prefed for 24 or 48 h with the dietary *B. thuringiensis* was not adversely affected. However, feeding on the same diets for 72 h was detrimental to the parasitoid because of premature host mortality. Continuous exposure of *H. armigera* larvae to the diets at different time intervals after parasitization (0, 4, or 6 d), prevented successful development and pupation of *M. croceipes*, mainly caused by early mortality of the host. Feeding parasitoid adults with *B. thuringiensis* preparations of subsp. *kurstaki* strain HD-73 mixed in honey was not harmful to the wasps. Moreover, Dipel or purified *B. thuringiensis* spores of HD-73, but not purified crystals of this strain, increased longevity of the wasps compared with the control (honey alone). Microscopic observations and color indications showed that the adult parasitoid ingested the honey with the Dipel. The incompatibilities between application of *B. thuringiensis* to host larvae and parasitization with *M. croceipes* are discussed with regard to combining microbial and entomophagous control strategies against *H. armigera*.

KEY WORDS *Helicoverpa armigera*, *Microplitis croceipes*, *Bacillus thuringiensis*, parasitoid, host–parasitoid–microbe interactions

THE ENDOPARASITOID *Microplitis croceipes* (Cresson) is a solitary parasitoid of larvae of heliothine spp. It is native on 2 of the most economically important pests in the United States, the corn earworm, *Helicoverpa zea* (Boddie), and the tobacco budworm, *Heliothis virescens* (F.) (Lewis and Brazzel 1966, Snow et al. 1966, King et al. 1985, King and Coleman 1989). *M. croceipes* can be an effective parasitoid because it is specific for heliothine spp., environmentally adaptable, tolerant of certain insecticide residues, and has a relatively high host search rate (Powell et al. 1986). Therefore, it may be useful for the biological control of *Heliothis* species (Knipling and Stadelbacher 1983). Recently, efforts have been made to develop mass-rearing methods for *M. croceipes* (Blumberg and Ferkovich 1994, Ferkovich and Blumberg 1994).

Helicoverpa armigera (Hübner) is an early-season (from early May to mid-July), polyphagous pest of vegetables and cotton in Israel and is the 1st lepidopterous pest to appear extensively on these crops. It is attacked by several local species of natural enemies, the most abundant of which is *Hyposoter didymator* Thunberg (Bar et al. 1979).

The biopesticide *Bacillus thuringiensis* Berliner, more than any other microbial pesticide, has attained wide commercial use against major lepidopterous pests, including *H. armigera* in Israel and heliothine spp. in the United States. The microbe formulations have great potential in integrated pest management (IPM) programs. They may be used to complement the effects of other biological control agents because of their environmental safety and pest selectivity (King and Coleman 1989). The combination of microbial insecticides with entomophagous control is an effective strategy in IPM programs which is used widely in bio-organic agriculture (Navon 1993).

Different effects of *B. thuringiensis* on natural enemies of insect pests have been reported. Wollam and Yendol (1976) reported satisfactory control of lepidopterous pests by integrating *B. thuringiensis* with a parasitoid. Several species of the egg parasitoid *Trichogramma* are known not to be affected by *B. thuringiensis* (Franz et al. 1980, Hassan 1983, Hassan et al. 1983, Oatman et al. 1983). According to Bull and Coleman (1985), microbial pesticides are fully compatible with releases of *Tri-*

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chogramma species. Hassan et al. (1983) reported that Dipel, among other insecticides, was harmless to most of the beneficials tested and can be recommended for use in integrated control programs. However, *B. thuringiensis* has been shown to affect certain parasitoids adversely by causing reduced parasitism (Vail et al. 1972), or by decreasing the number of parasitoids emerging from *B. thuringiensis*-infected hosts (von Hamed 1979, Temerak 1980).

Microplitis croceipes was introduced into Israel from the United States (Gainesville, FL) in 1993 to improve the biological control of *H. armigera* but so far has not been released in the field. One reason for this is the lack of inexpensive technology for mass propagation of the parasitoid (King and Coleman 1989, Ferkovich and Blumberg 1994). However, in view of the diverse reports on the effects of *B. thuringiensis* on natural enemies, and to develop biological control strategies against moth pests, we thought that before initiating large-scale releases of the parasitoid against heliothine pests in Israel, it would be useful to study the interactions among *M. croceipes*, its host *H. armigera*, and *B. thuringiensis*. Studies in the current work included effects of microbe preparations on host larvae, on *M. croceipes* oviposition, on immature parasitoids, and on adult longevity.

Materials and Methods

Insect Source. The *H. armigera* colony has been maintained on a diet (Navon et al. 1990) for the last 5 yr. Third-instars 10–12 mm in size weighing 10.2 ± 0.7 mg (mean ± SE), with a head capsule width of 1.05 ± 0.03 mm, were used in all experiments. The *M. croceipes* colony originated from cocoons obtained in 1993 from a culture that had been maintained on *H. zea* in the Center for Medical, Agricultural and Veterinary Entomology, USDA–ARS, Gainesville, FL. The parasitoid was reared on *H. armigera* according to procedures outlined by Powell and Hartley (1987). Adult parasitoids were kept with honey and water in plastic cages (35 by 30 by 15 cm) at 24 ± 2°C, 50–60% RH, and a photoperiod of 16:8 (L:D) h.

Feeding *H. armigera* Larvae with Dietary *B. thuringiensis*. Larvae were exposed to diets with *B. thuringiensis* according to the bioassay procedure of Navon et al. (1990). Dilution series of a commercial wettable powder of Dipel 16,000 IU/mg *B. thuringiensis* subsp. *kurstaki* strain HD-1 (Abbott, North Chicago, IL) in distilled water with 0.05% polysorbate 80 were incorporated into the diet at 45°C and mixed with a laboratory stirrer. The diet with the Dipel was poured into a sterile plastic petri dish with a grid forming 21 rearing cells. Controls consisted of diets of the aqueous mixture without the microbial product. After diet setting, a single 3rd-instar was put in each cell. Larvae were reared on the diet for different periods of time, after which they were exposed to the parasitoid.

Effect of *B. thuringiensis* on Parasitoid Oviposition. Host larvae fed on diet with 0.08 or 0.16 mg/g *B. thuringiensis* for 24 h (n = 36 and 20, respectively), on diet with 0.08 mg/g *B. thuringiensis* for 48 h (n = 18), or on diet only (control) (n = 63) were exposed in petri dishes to female parasitoids (8–10 host larvae per 5 females) for 1 h. Preliminary observations showed that feeding *H. armigera* larvae on diet with 0.16 mg/g *B. thuringiensis* for 48 h resulted in such high mortality rates of the larvae that any recording of parasitoid oviposition were precluded. After removal of the wasps, the host larvae were dissected, and the number of parasitoid eggs per host was determined. Dissection was done in a drop of saline solution on a glass slide under a binocular microscope. The wasp eggs were easy to locate because they usually floated out of the host's hemocoel (Blumberg and Ferkovich 1994).

Effect of *B. thuringiensis* on Parasitoid Immatures. Two experiments were carried out. In the 1st, the effect of *B. thuringiensis*, applied to the host before parasitization, on parasitoid pupation and host mortality was studied. Larvae of *H. armigera* were fed on diets with 0.08 or 0.16 mg/g *B. thuringiensis* for 24 h (n = 60 for each concentration), on diets with 0.08 and 0.16 mg/g *B. thuringiensis* for 48 h (n = 52 and 48, respectively), or on diets with 0.08 and 0.16 mg/g *B. thuringiensis* for 72 h (n = 15 and 16, respectively). After feeding, host larvae were exposed for oviposition by *M. croceipes* as described above. After removal of the wasps, host larvae were individually placed in cups containing diet only.

The effect of Dipel on unparasitized host larvae also was studied. In the control, host larvae were not exposed to *B. thuringiensis* before parasitization. In the 2nd experiment, the effect on the development of *M. croceipes* of a 0-, 4-, and 6-d interval between parasitization and continuous exposure of host larvae to *B. thuringiensis*, was studied. *H. armigera* larvae were 1st exposed to oviposition by *M. croceipes* as described above, then placed individually in cups containing *B. thuringiensis* diet at concentrations of 0.08 or 0.16 mg/g, or diet only (control). This was done immediately after removal of the wasps, after 4 d, and after 6 d. In the control, host larvae were kept after parasitization on diet only. Symptoms of intoxicated host larvae were described, and larval weight gain was evaluated. The percentages of host mortality, parasitoid pupation, and duration of parasitoid egg-larval stage in the 2 experiments, were assessed daily.

Effect of *B. thuringiensis* on Longevity of Adult Parasitoid. *Microplitis croceipes* adults were offered honey mixed with 1% of the following microbe sources: Dipel WP (wettable powder, 16,000 IU/mg), and spores and crystals of *B. thuringiensis* subsp. *kurstaki* HD-73. This strain was isolated from culture grown on peptonized milk medium at 28°C for 72 h (Ibarra and Federici 1986). The crystals were separated from spores with a biphasic liquid

separation system used previously (Navon et al. 1993). Newly emerged parasitoid adults were placed individually in closed and ventilated vials (90 by 23 mm) that contained honey alone or a mixture of honey with 1 of the above microbe sources. In the control, adults were not offered any food. Mortality of adult parasitoids was recorded daily.

In separate experiments, acquisition of food with *B. thuringiensis* by adult parasitoids was checked as follows: the honey-*B. thuringiensis* mixtures were mixed with 0.05% of a red food dye, Amaranth (C.I. No. 16185, S. No. 212, E. Merck, Darmstadt, Germany). Two series of 4 single, newly emerged *M. croceipes* adults were used in 5 replicates. In one series, the observations were made on live wasps; in the other, on parasitoid adults which had been dead for 48 h. After surface washing of the insects with distilled water, the color of the digestive tract was examined under a binocular microscope (40× magnification). To evaluate ingestion of *B. thuringiensis* materials by the adult parasitoid, the abdomen single live or 48-h-dead insects was surface washed for 5 min with 70% aqueous ethyl alcohol, blotted dry on sterile tissue paper on a microscope slide, and observed under a microscope (400× phase contrast magnification) for mature vegetative cells of *B. thuringiensis* containing spores and crystals.

Statistical Analysis. Data were analyzed statistically using 1-way analyses of variance (ANOVAs) followed by mean separation with the Neuman-Keuls test on the Epistat computer program.

Results

Effect of *B. thuringiensis* on Parasitoid Oviposition (Fig. 1). The mean number of parasitoid eggs per host did not differ significantly in host larvae which before parasitization had been fed for 24 or 48 h on a diet containing 0.08 mg/g Dipel, for 24 h on a diet containing 0.16 mg/g Dipel, or on diet only (control). Therefore, these results indicate no adverse effects of *B. thuringiensis*-induced toxicosis on the acceptance of *H. armigera* for oviposition by *M. croceipes*.

Effect of *B. thuringiensis* on Parasitoid Immatures. Feeding *H. armigera* larvae before parasitization (Fig. 2) on diet containing lethal concentrations (0.08 mg/g or 0.16 mg/g) of Dipel for 24 or 48 h, and transfer of the parasitized larvae to an untreated diet immediately after parasitization did not prevent the development of *M. croceipes* immatures. The percentages of mortality of host larvae and parasitoid pupation, in these cases, did not differ significantly from those recorded in the control (diet only). Successful parasitoid development, therefore, was not adversely affected. However, prolongation of the feeding period on a diet containing the same concentrations of Dipel for 72 h before parasitization resulted in a significant increase in host mortality at the 0.16 mg/g dose, and

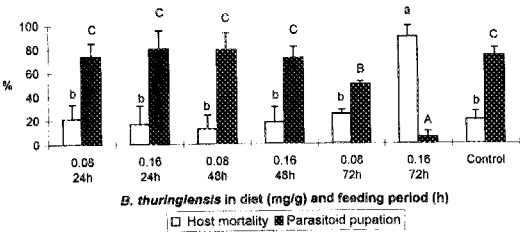

Fig. 2. Development of *M. croceipes* in larvae of *H. armigera* prefed with dietary *B. thuringiensis* and host mortality. Means designated by a common lower-case letter and separately by an upper-case letter do not differ significantly ($P > 0.05$).

in a significant reduction in parasitoid pupation at both the 0.08 and 0.16 mg/g doses. In the 72-h exposure, percentage pupation was lower and percentage host mortality was higher after feeding on the 0.16 mg/g Dipel diet, compared with the 0.08 mg/g Dipel diet (Fig. 2). Symptoms of intoxicated hosts included sluggish movements of larvae and reduced feeding, which was expressed by lower weight gain of the *B. thuringiensis*-fed larvae. On day 4, the weight of larvae fed on 0.08 and 0.16 mg/g dietary Dipel was 14.0 ± 1.5 mg ($n = 15$) and 13.4 ± 0.7 mg ($n = 15$), respectively. In the control, larval weight was 56.4 ± 5.6 mg ($n = 15$), which is ≈4 times higher than in the Dipel-fed larvae.

Continuous exposure of *H. armigera* larvae to a diet containing 0.08 or 0.16 mg/g *B. thuringiensis*, immediately after parasitization, resulted in complete mortality of host larvae within ≈6 d after the exposure (Table 1). None of the parasitized hosts which fed on the above diets enabled development of parasitoid immatures. Lower mortalities were

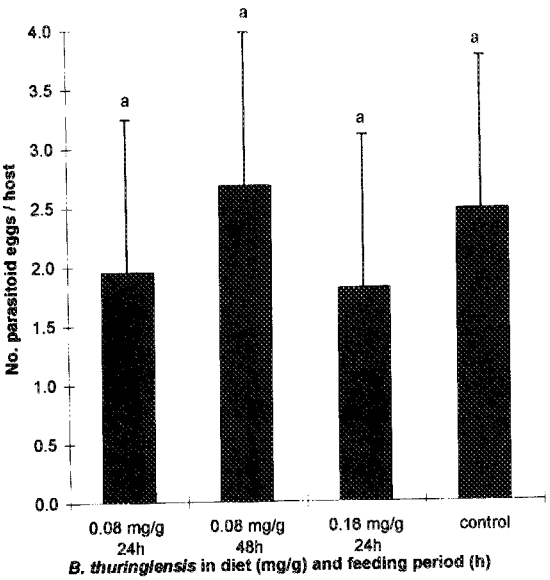

Fig. 1. Oviposition of *M. croceipes* in larvae of *H. armigera* prefed with dietary *B. thuringiensis* for 24–48 h.

Table 1. Effects of *B. thuringiensis*, applied at different times after parasitization, on *H. armigera* larvae and its parasitoid *M. croceipes*

Days from parasitization to *B. thuringiensis* exposure of host	Dipel concn, mg/g	Host				
		No. exposed to parasitoid	Longevity, d mean ± SD	*n*	% mortality	% parasitoid pupation
0	0.08	47	6.5 ± 1.8a	50	100a	0b
—	0.08	Not exposed	8.0 ± 3.6a	45	37.0b	—
0	0.16	50	5.6 ± 0.8a	50	100a	0b
—	0.16	Not exposed	7.0 ± 3.1a	45	78.0a	—
0	Control	50	14.7 ± 3.8b	3	6.0b	94.0a
4	0.08	37	13.4 ± 4.9b	35	94.6a	5.4b
	0.16	39	10.6 ± 2.3b	39	100a	0b
	Control	39	15.8 ± 5.9b	5	12.8b	87.2a
6	0.08	40	16.5 ± 3.4b	34	85.0a	15.0b
	0.16	40	14.2 ± 1.8b	40	100a	0b
	Control	40	24.0	1	2.5b	97.5a

Means for each parameter within each time interval followed by a common letter are not significantly different ($P < 0.05$).

obtained when host larvae were fed on dietary *B. thuringiensus* without exposure to the parasitoid. Larval development of *M. croceipes* in hosts fed on diet only (control) was accomplished within 12–13 d ($n = 120$), after which the host remained alive for few more days (see also Bryan et al. 1969). Continuous exposure of *H. armigera* to dietary *B. thuringiensis* 4 and 6 d after parasitization also resulted in high rates of host mortality (94.6 and 85.0%, respectively) in hosts fed on a diet containing 0.08 mg/g Dipel and 100% in hosts fed on a diet containing 0.16 mg/g Dipel. Feeding host larvae on a diet with 0.08 mg/g Dipel in the 4- and 6-d experiments resulted in a low rate of parasitoid pupation (5.4 and 15.0%, respectively). However, no parasitoid pupation was recorded in host larvae that were fed on the 0.16 mg/g *B. thuringiensis* diet. In the 4- and 6-d experiments, host larvae lived longer but percentage host mortality did not differ significantly when the larvae fed on a diet containing 0.08 mg/g of *B. thuringiensis* compared with diet that contained 0.16 mg/g of the microbial product (Table 1). In the 4-d experiment, only 1 of 2 individuals that pupated yielded an adult parasitoid. In the 6-d experiment, 6 individuals completed larval development and pupated. The duration of the egg–larval stage of these 6 individuals was 13.3 ± 0.5 d, which did not differ significantly from that recorded in the control (13.2 ± 1.6 d, $n = 39$). Four of the 6 pupae completed their development to the adult stage. This rate of adult emergence (67.0%) was similar to that recorded in the control (66.7%, $n = 39$). The duration of the pupal stage of the 4 individuals in the 6-d experiment also was similar to that recorded in the control: 12.0 ± 1.2 versus 10.5 ± 1.1 d ($n = 26$), respectively.

Effect of *B. thuringiensis* on Longevity of Adult Parasitoid. Observations on adults fed honey containing the dye Amaranth revealed the appearance of the red dye in the digestive tract, indicating that the honey with the Dipel or the spores and crystals of HD-73 were ingested by the wasps. Digestive tracts of adults fed on honey–*B. thuringiensis* combinations without the dye evinced their natural yellow color. Microscopic observations showed that the adult abdomen of live parasitoids feeding on the honey–*B. thuringiensis* preparation did not contain vegetative cells of the bacterium. However, such vegetative cells with crystals and spores were found in the digestive tract of all the parasitoid adults on the 2nd d after their death. Adults feeding on crystals only did not show vegetative growth because spores were not present in the microbe preparation.

None of the honey–*B. thuringiensis* combinations (1% Dipel, 1% spores, 1% crystals, or 1% spores + crystals) was harmful to *M. croceipes* adults, because longevity was not adversely affected by their presence in the food (Fig. 3). The differences in adult longevity caused by the microbe preparations were small, ranging between 10 and 20%. The presence of spores in the adult diet increased adult longevity, but the crystals (purified δ-endotoxin) did not cause this effect. Feeding the adults with

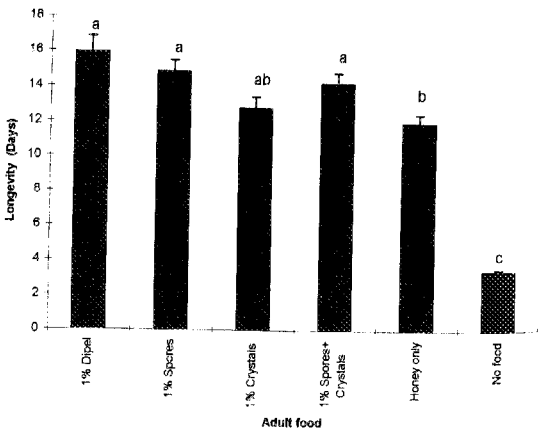

Fig. 3. Longevity of *M. croceipes* adults fed with mixtures of honey and *B. thuringiensis* preparations. Means designated by a common letter do not differ significantly ($P > 0.05$).

Dipel resulted in a significant increase (20%) in their longevity compared with feeding on honey alone. Starvation caused a reduction in longevity to ≈1/4 of the parasitoid life span with honey.

Discussion

Oviposition of *M. croceipes* was not prevented in larvae of *H. armigera* prefed with lethal doses of *B. thuringiensis*. This suggests that under the conditions studied, symptoms of *B. thuringiensis* intoxication in host larvae, such as feeding reduction and weight loss (Navon et al. 1993), cannot be detected by the parasitoid female as an indication that oviposition in such infected hosts would not lead to successful parasitism. In practical terms, the inability of the parasitoid to discriminate between healthy and infected hosts may cause some waste of eggs; consequently, both the reproduction and efficacy of the parasitoid can be affected adversely.

Feeding *H. armigera* larvae before parasitization on a diet containing 0.08 or 0.16 mg/g *B. thuringiensis* for 24 or 48 h was not harmful to the host or to the parasitoid. However, prolongation of the feeding period on those diets to 72 h had adverse effects on parasitoid development resulting from an increase in host mortality caused by the microbial product. Successful parasitism of *M. croceipes* in *H. armigera* larvae fed on *B. thuringiensis* before parasitization seems to depend on the duration of exposure of the host and the microbial product, as well as on the ability of the host to survive after feeding on dietary *B. thuringiensis*.

The inability of *M. croceipes* to complete larval development in host larvae that were fed continuously after parasitization on dietary *B. thuringiensis* is explained by the early mortality of the host caused by the spore–crystal product (Dipel) in the diet. The longer survival of host larvae in the 4- and 6-d experiments, and the higher percentage of parasitoid pupation in the 6-d experiment (Table 1), could be explained by lower consumption of *B. thuringiensis* by larvae reaching a more advanced stage of parasitism, or other mechanism(s) resulting from parasitism that slowed the intoxication process of *B. thuringiensis* in the parasitoid larvae. The results shown in Table 1 suggest that if *H. armigera* larvae are exposed continuously to dietary *B. thuringiensis*, the rate of prevention of parasitoid development is high (85–100%) and renders parasitism ineffective. In a parasitized host exposed to *B. thuringiensis* immediately after parasitization, premature host death is probably the reason for the complete mortality of parasitoid immatures. A considerable host mortality (78%), which is caused by *B. thuringiensis* (Table 1) in unparasitized hosts, may limit the reproduction of *M. croceipes*. In the 4- and 6-d experiments, host mortality is responsible for the unsuccessful development of the parasitoid, whereas the direct effect of *B. thuringiensis* on parasitoid immatures seems less probable. Although only a few parasitoid larvae developed successfully in hosts exposed to *B. thuringiensis* 6 d after parasitization, the duration of both the egg–larval and pupal stages in infected hosts did not differ from those in uninfected hosts. This is an indication that the bacterium adversely affects the host rather than the parasitoid. Similarly, Thoms and Watson (1986) demonstrated that immature stages of the ichneumonid parasitoid *Hyposoter exiguae* (Viereck) completed their development in *B. thuringiensis*-infected hosts if hosts did not die prematurely. They also concluded that applications of the microbe under field conditions would probably adversely affect immature *H. exiguae* more than adults. Salama et al. (1982) reported a reduction in percentage of emergence and reproductive potential of *Microplitis demolitor* Wilkinson when its host larvae were fed on a *B. thuringiensis* diet.

The significant increase in longevity of adults that were fed on Dipel mixed in honey may result from fermentation residues in the microbial product that provided nutritional support for adult longevity. A similar effect, which cannot be explained at this stage of the study, was caused by purified spores of *B. thuringiensis* strain HD-73.

Wysoki (1989) reported no adverse effect of a commercial preparation of *B. thuringiensis* (Dipel) on 2 encyrtid wasps—*Arhopoideus* (*Hungariella*) *peregrinus* (Compere) and *Anagyrus fusciventris* (Girault). Not only was the preparation harmless, but the mortality of the wasp was delayed, probably because of additional food ingredients in the product. The parasitoid wasps were observed in the avocado orchards 7 d after initial treatment with *B. thuringiensis* (Wysoki et al. 1975). Dunbar and Johnson (1975), however, reported that ingestion of the active material in sugar water by the parasitoid *Cardiochiles nigriceps* Viereck resulted in a significant decrease in post-treatment longevity. Salama et al. (1991) found that in the interaction between the Indianmeal moth, *Plodia interpunctella* (Hübner), and the parasitoid *Bracon brevicornis* Wesmail, percentage of adult emergence and longevity of the female parasitoid were reduced with the increase of *B. thuringiensis* concentrations.

Our findings that under certain laboratory conditions *B. thuringiensis* may be harmful to *M. croceipes* immatures (mainly through its detrimental effect on the host), but not to the adult parasitoid, suggest that in an IPM program for heliothine spp. with *M. croceipes*, the use of *B. thuringiensis* may limit the buildup of natural enemies of the parasitoid. However, *M. croceipes* may prove effective against 3rd and 4th instars of the host that escaped as neonates from *B. thuringiensis* application in the field.

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